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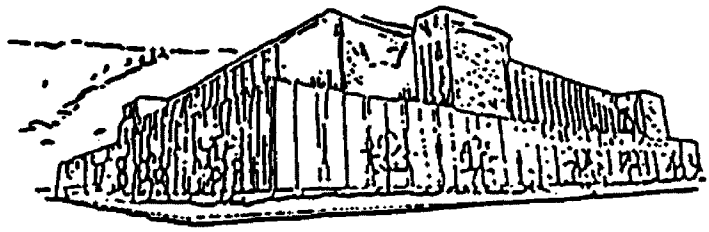
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Risk-sensitive foraging in rats:

The effects of response-effort and reward-amount manipulations

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Presented in partial fulfillment of the

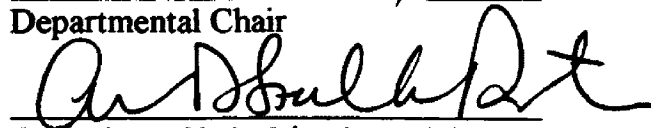
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Risk-sensitive foraging in rats:

The effects of response-effort and reward-amount manipulations

Committee Chair: Allen Szalda-Petree, PhD.



Evidence for risk sensitivity as a function of a changing energy balance has been documented in small avian and mammalian species. However, most research fails to produce risk sensitivity and argues that organisms are universally risk prone when presented with variable delays but invariable reward amounts. Manipulations in response effort have been relatively neglected, and this may explain the apparent rarity of risk sensitivity in past research. Fitness of an organism depends upon the economic relationship between caloric gain and energy expenditure. Therefore, in order to effectively investigate foraging, shifts in response effort and reward amount must be used to deplete an organism's energy state. A choice preparation using wheel running in rats examined risk-sensitive preferences when both response effort and reward amount were manipulated. Concurrent reinforcement schedules (FI/60 and VI/60) yielded equivalent food amounts per unit time in all treatments. Two levels of response effort (20 g or 120 g tangential resistance) and two levels of reward amount (3 or 9 pellets) were combined to form four distinct response-effort/reward-amount pairings. Increasing reward amounts significantly shifted choice toward the FI schedule in both response-effort conditions. The incidence of choice preference and the magnitude of shifts in choice were greater for the high response-effort conditions than for the low response-effort conditions. Implications of the significant interaction between response effort and reward amount are discussed in terms of a general energy-budget model.

Table of Contents

Introduction	1
Methods	12
Results	16
Discussion	18
References	25
Appendix (Full Literature Review).....	30
Appendix (References for Literature Review).....	66

Introduction

In order to survive and reproduce, an animal must obtain sufficient resources. The relationship between foraging and fitness is dependent upon environmental constraints, and foraging strategy is dependent upon the economic relationship between energy expenditure and caloric gain. In the past, research has been aimed at dissecting the factors determining efficient foraging strategies, or what is called 'optimal foraging.' Optimal foraging theory assumes that fitness will be maximized by natural selection, and that fluctuations in the environment over a period of time may dictate a change in foraging strategy. In theory, the maximization of fitness will result in the maximization of foraging efficiency. Physical effort exerted during foraging, time to next food reward, distance between food patches, and overall caloric expenditure have been examined in this context (Appelzweig 1951; Cheloni et al., 1998; Collier, Hirsch, Levetsky, and Leshner; 1973; Haddad et al., 1994; Keehn, 1981; Mitchell & Brenner, 1997). It remains unclear whether a single model can predict foraging behavior as a function of environmental factors. When two food sources yield equivalent reward amounts yet differ in payoff variances organisms will develop a preferential pattern of choice. Risk-sensitive foraging theory (Caraco, 1980; 1981; Caraco, Martindale, Whittam, 1980; Kacelnik & Bateson, 1996; Kamil & Roitblat, 1985; Stephens, 1981; Stephens & Charnov, 1982; Stephens & Krebs, 1986) states that an organism demonstrating a preference for a constant option over a variable

option is averse to the risk of starvation while a risk-prone organism displays a preference for a variable option. Researchers have examined foraging preferences in terms of variance in the quality of food (Tuttle, Wulfson, & Caraco, 1990), the quantity of food (Bateson & Kacelnik, 1995; Caraco 1980, 1981, 1982, 1983; Hamm & Shettleworth, 1987; Kagel, et al., 1986; Wunderle, Castro, & Fetcher, 1987), and variances of the delay to the next rewarding event (Bateson & Kacelnik, 1995, 1997; Stephens & Charnov, 1982). Several studies have explored novel foraging situations, such as manipulations of metabolic rate as a result of weather changes (Caraco, Kacelnik, Mesnik, & Smulewitz, 1992; Ha, 1991; McNamara, 1996), the influence of gestation on foraging (McNamara, Merad, & Houston, 1996), migration (Bednekoff & Houston, 1994), and socialization (Caraco, Utez, Gillespie, & Giraldeau, 1995). In some scenarios, it is more adaptive for the animal to obtain food quickly and minimize the time delays between eating. In other situations, it seems that a less impulsive animal would fair better by waiting for food rewards of a more preferred amount.

Beginning in the early 1980's, research examined the parameters of foraging behavior when the organism was presented with variable verses constant food sources (Caraco, 1980; Stephens, 1986; McNamara, 1982). It has become clear that foraging is limited by the accessibility of resources (e.g. Caraco, 1981), time constraints (Houston & McNamara, 1982), variability in the amount and time to the next rewarding event (Tuttle, Wulfson, & Caraco, 1990), and the organism's energy

reserve (Barnard & Brown, 1985), but it is still unclear how these factors interact. The forager is faced with a complex problem when both delay to reward and reward amount vary concurrently. Researchers have argued that foraging animals formulate a set of rules based upon past experience (Benson & Stephens, 1996; Caraco, 1980, 1981; Caraco, Kacelnik, Mesnik, & Smulewitz, 1992; Houston & McNamara, 1982; Kacelnik & Bateson, 1996; Kamil & Roitblat, 1985; Pyke, 1984; Real & Caraco, 1986). According to Caraco (1980; variance discounting rule) and Stephens and Charnov (1982; z-score model), foraging rules are calculated by accounting for delay to reward and reward amount variances. Both models predict for the occurrence of risk-sensitive foraging as a function of interacting environmental constraints and the possibility of overnight starvation.

In two experiments with dark-eyed juncos (*Junco heymalis*), Caraco (1981) discovered that the constant reward was preferred when food intake exceeded energy expenditure (a positive energy balance) and the variable reward was preferred when the subject's energy budget was negative. Other researchers have modeled the influence of a daily energy budget model on risk-sensitive foraging (Houston, 1991; MacNamara & Houston, 1992; Stephens, 1981). It seems counterintuitive that an organism would deliberately increase its vulnerability to starvation when energy stores are low by behaving in a risk-prone manner; however, a more variable alternative will occasionally yield a larger supply of food. Therefore, a run of good luck could solve

the crisis of a negative energy balance and replenish energy reserves.

Two classic investigations demonstrated increasing risk-prone choice behavior as a result of diminishing reward amounts. Barnard and Brown (1985) tested risk sensitivity in common shrews (*Sorex araneus*) using concurrent feeding sites, one fixed amount and one variable. The transition from risk-aversion to risk-proneness occurred when the shrews were fed an amount that was below their physiological requirement. Stephens and Paton (1986) placed six wild-caught Rufus hummingbirds (*Selasphorus rufus*) in a free choice preparation in which one option yielded a high mean amount with a high variance whereas the other yielded a low mean amount with a low variance. Risk-prone tendencies were observed in the low-line treatment, and preferences shifted to the more constant alternative (the low-variance condition) when reward amount was increased.

Some recent models of risk-sensitive foraging place less emphasis on energy states and stress the importance of cognitive processes on the development of foraging strategy. The organism will depend upon representations of food variances in order to compute foraging decision rules. It is assumed that decision rules serve an adaptive function by increasing the probability of survival. Kacelnik and Bateson (1996) suggest that cognitive and behavioral ecology approaches be fused to understand the decision rules animals generate while foraging. The researchers state that when risk is a result of variability in the amount of reward, animals most frequently display risk-averse

preferences. Alternatively, if the variability lies in the delay to reward, animals are universally risk prone (Bateson & Kacelnik, 1995, 1997; Caraco et al., 1992; Kacelnik & Bateson, 1996).

Risk-sensitive foraging theory is acknowledged by Kacelnik and Bateson (1996) as the most accurate and current method of understanding how an animal's energy budget will affect choice performance. In addition to this, the authors have combined an information processing approach with Weber's law in order to account for risk sensitivity. Weber's law provides the foundation for a theoretical framework known as scalar expectancy theory (SET) that accounts for time variables (Gibbon, 1977, as cited in Kacelnik & Bateson, 1995). Reborda and Kacelnik (1991) have expanded SET to include representations for variability in reward amount as well as in delay to reward, thus predicting for bi-directional foraging strategy. The value remembered for an interval or amount is represented as a normal distribution. Each subsequent trial is compared with the distribution and a choice is made according to an expected gain or loss. SET predicts for nearly exclusive choice preference by an organism (either risk-prone or averse), depending upon whether delay or mean amount is varied. Specifically, SET predicts that variability in delay should be preferred because the variable option often will yield shorter delays without compromising long-term gains. Variability in amount, on the other hand, should be avoided because the probability of the constant option reoccurring is much higher than the probability of

the variable amount reoccurring.

Bateson and Kacelnik (1995) found evidence for SET using starlings (*Sturnus vulgaris*). The results showed that the subjects preferred variable delays when reinforcement amounts were equivalent, and variance in amount was avoided when the delays were the same. Furthermore, the researchers have demonstrated that starlings behave in a risk-prone manner when delay is manipulated even when the rewards obtained are increased. Counter to the predictions of the energy-budget rule, no effect of energy budget on performance occurred (Kacelnik & Bateson, 1997).

Most of the research on risk-sensitive foraging has employed small avian species, but investigations involving larger mammals are also represented. Experiments involving rats on various concurrent time schedules have shown either constant risk aversion (Logan, 1965; Rider, 1983; Battalio, Kagel, & MacDonald, 1985; Kagel, MacDonald, Battalio, White, & Green, 1986; Hastjarjo, Silerberg, & Hursh, 1990) or constant risk proneness (Logan, 1965; Pubols, 1962; Rider, 1983), independent of energy state. Zabludoff, Wecker, and Caraco (1988) found evidence of risk sensitivity when body mass was manipulated below 85% ad-lib mass, but as Kacelnik and Bateson (1996) have acknowledged, the data obtained were confounded by an increase in the variability of the risky option as body mass decreased. Past experimentation with rats has typically employed the discrete lever-press response, and has failed to explore other forms of operant/instrumental behavior.

Timberlake (1994) examined a variety of behaviors, from appetitive to aversive, in diverse species. At the 'systems' level, appetitive behaviors such as predation can be divided into 'subsystems' (general search, focal search, and handle/consume). For the most part, behavioral ecologists working in laboratories have been successful at allowing the organism under study to engage in each of the subsystems involved in foraging. Experimental psychologists, on the other hand, have been less successful at this task by focusing on only a portion of the subsystems involved, usually targeting only 'focal search' and 'handling' mode in limited types of species. Experiments examining risk sensitivity in rats, as stated above, typically used a lever-press response and a discrete-trials preparation. A lever press requires only an instantaneous response, and according to the behavioral systems analysis (Timberlake, 1994) is representative of focal search and handling. Given a liberal reinforcement schedule with a lever-press response, the subject has several seconds, and in some cases minutes, before the delivery of food reward. Thus, the behavior that immediately follows a lever press is neglected by the researcher.

The caloric cost of producing a response within a foraging preparation may be a crucial variable determining the foraging strategy employed by the organism. Response cost and response effort have been explored within a lever-press choice preparation (e.g. Alling & Poling, 1995; Keehn, 1981; respectively); however, response effort has received much less attention compared with response cost. The

duration and continuity of response is minimal in a lever-press situation, even when response effort is increased. Running may be a more appropriate tool in the investigation of foraging because response effort can be manipulated by increasing the amount of resistance during a trial (Collier et al., 1973; Haddad et al., 1994) without compromising the duration or uniformity of the response.

Several field studies have outlined other factors influencing risk sensitivity. Caraco, Uetz, Gillespie, and Giraldeau (1995) found that an individual's resource consumption is dependent upon the size of its social group. The researchers discovered that an individual spider's food consumption is inversely proportional to colony size, thus risk sensitivity is modulated by the formation of a social group. Similar functions are apparent among social groups that form inconsistent social bonds. Some ethologists suggest that migratory birds form a more cohesive social network while migrating than while not migrating. Bednekoff and Houston (1994) found that risk proneness in yellow-rumped warblers (*Dendroica coronata*) facilitated premigratory fattening. In contrast, the birds exhibit risk-averse tendencies during the rest of the year, when they are not migrating. These examples from the field indicate that a common construct that accounts for caloric cost, in terms of the response effort expended during foraging, may be an important factor in determining a given foraging strategy.

The recent literature surrounding risk sensitivity has demonstrated that the

degree to which an animal behaves in a risk-averse or risk-prone manner depends on whether time or amount is experimentally manipulated (Caraco et al., 1992; Kacelnik & Bateson, 1996). When variability is generated by the delay to reward, animals are risk prone, and the degree of risk proneness is relatively unaltered by manipulations of the energy budget. Alternatively, when variability is generated by the amount of reward, animals are usually risk averse, and there is some evidence that the organism's energy budget affects preference (Kacelnik & Bateson, 1996). There exist many gaps in the literature, and it is necessary to compare the effects of delay and amount in the same species under consistent experimental preparations. The effects of energy-budget manipulations have fueled much of the interest in risk. A closer examination of the underlying ecological, physiological, and psychological processes contributing to foraging may prove to be profitable adventures in a joint quest to understand foraging behavior. Although models such as SET and Weber's law help to provide us with possible cognitive explanations of foraging theory, they fall short of describing stochastic strategy. Therefore, as Smallwood (1996) has suggested, perhaps we should return to the basics of foraging theory and explore economic models further before turning to less parsimonious explanations of behavior.

The review conducted by Kacelnik and Bateson (1996) illustrates that few studies have demonstrated risk-sensitive foraging. Studies conducted with relatively large animals with lower mass-specific metabolic rates have failed to show risk

sensitivity when energy reserves are manipulated. Larger animals have a larger energy reserve and may not be susceptible to minor changes in experimental procedure aimed at shifting preference; however, manipulating response effort may help overcome the hurdle of large energy reserves. In the behavioral ecology literature, there has been no research directly aimed at examining the effects of effort on risk sensitivity, and effort may prove to be a critical variable in determining an organism's energy balance.

The present design is intended to manipulate an organism's energy balance by varying both response effort and reward amount. A running wheel choice preparation is utilized in which four distinct response-effort/reward-amount combinations are manipulated, each combination specific to a certain phase: (1) low-effort/small-reward, (2) high-effort/small-reward, (3) high-effort/large-reward, and (4) low-effort/large-reward. A final phase was necessary to ascertain whether the effects witnessed by changing environmental demands were absolute rather than being representative of order effects. Therefore, phase five entirely reinstated the parameters of phase one.

If SET holds true, then the subjects should prefer the variable-delay option across all phases, regardless of experimental manipulations that are intended to alter the energy balance. When the effort required to make a response is increased, the energy balance should be impacted according to a daily energy budget rule. Risk-prone tendencies should be exacerbated due to the increasing cost associated with obtaining rewards in high-response effort conditions. Furthermore, if a daily energy budget rule

is applicable, then as the energy budget is made positive by increasing the amount of food received per reinforcing event, the subjects should behave in a risk-averse manner and prefer constant delays.

Methods

Subjects

Twelve naïve, male Sprague-Dawley rats, approximately 90 days old at the beginning of the experiment were used. Upon arrival at the laboratory the rats were provided with ad-lib water and food for seven days. They were maintained at approximately 85% of their pre-deprivation individual body mass for the duration of the experiment. Water was continuously available in the home cage and the animals were fed daily the appropriate amount of Purina Rat Chow approximately one hour after the last subject had finished its session.

Apparatus

Two Wahman running wheels were modified to allow computer monitoring of wheel movement. This was accomplished through a computer mouse attachment to the wheel axle via a system of reduction pulleys (Petree, Haddad, & Berger, 1992; Szalda-Petree, Karkowski, Brooks, & Haddad, 1994). Response effort was manipulated by applying pressure, via an adjusting tensioning bar, on a 7.62-cm aluminum disc approximately 1.3 cm thick that was attached to the wheel axle protruding from the non-movable side of the wheel (Haddad et al., 1994).

A Lexan choice box (23 cm X 23 cm X 23 cm) was placed between the two wheels and linked to each wheel via a 12 cm-long tunnel 8 cm in diameter. Reinforcers were delivered to the food cup located along the forward wall of the choice box,

equidistant from both running wheel entrances. Small 2.5 mV lamps (1 cm in diameter X 2 cm long) were located above the entrances to each tunnel. Each pair of wheels and their accompanying choice box was housed in a large (0.6 m X 0.6 m X 1.2 m) sound-attenuated cabinet with a blower to provide ventilation and masking noise.

Procedure

Subjects first received magazine training in which each subject was confined to a single wheel where pellets were delivered on a VT 25-s schedule for six 15-min sessions. The specific running wheel in which the subject received magazine training was alternated per session to avoid the development of a side/wheel bias. After six sessions, single-wheel run training was conducted using a FR schedule that was gradually increased from 5 to 300 cm. Again, the wheel in which the run training occurred alternated daily. Following four sessions of single-wheel run training, the choice box was inserted and the subjects received two additional single-wheel run training sessions in which reinforcement was delivered in the choice box. Then, the pathways from both running wheels were opened to the choice box during double-run training. Subjects were allowed to move between wheels, receiving reinforcement on concurrent FR 300 cm schedules for four consecutive sessions. Upon completion of the double-wheel run training, phase one of the experiment began.

The experiment consisted of five phases in which response effort (20 g or 120 g tangential force required to move the wheel) and reward amount (3 or 9 pellets)

were varied (see table one) using a concurrent FI 60-s: VI 60-s schedule (Fleshler & Hoffman, 1962). The schedules were pseudo-randomly assigned to the running wheels to control for a possible position bias, such that no running wheel was associated with a given schedule for more than two consecutive sessions. A 2.5 mV lamps signaled either the FI 60 or the VI 60 schedule, these were counterbalanced, resulting in the lamp signaling the FI schedule for half the subjects and the VI schedule for the remaining subjects.

A particular schedule was chosen when any running (1 cm or greater) was detected in the associated wheel. The alternate schedule/wheel was then made unavailable, by engaging a braking system, until reinforcement was obtained from the selected wheel. The distance requirement (ratio length) for reinforcement under both schedules was 90 cm (3/4 rotation of the wheel). A 5 s inter-trial interval (ITI) was used during which both wheels were braked. Each phase continued until stable choices, defined as no upward or downward trend in choices across four consecutive sessions, were obtained. Small reward-amount sessions lasted for 50 trials (phases one, two, and five). Within the large reward-amount conditions (phases three and four), the subjects would approach satiation as the session progressed and would discontinue running. Therefore, sessions were limited to 50 trials or 50 min, whichever occurred first.

Table one: Response-effort/reward-amount combinations per experimental phase.

Phase	I	II	III	IV	V
Response effort (g tangential force)	20	120	120	20	20
Reward amount (# of food pellets)	3	3	9	9	3

Note. All twelve subjects Ss experienced each phase in the same order.

Results

The number of reinforcing events associated with the FI schedule was divided by the total number of reinforcing events in order to provide a percentage of FI choice for each session. The final four days of each phase were averaged to provide a percentage of choice for each phase. As can be seen in table two, increasing the reward amount within the high-response effort conditions produced the greatest shift in choice behavior, with a strong VI choice (risk-proneness) in phase two and strong FI choice (risk-aversion) in phase three. Relative shifts in VI choice behavior were apparent between the low-response effort conditions, phases one and four.

Table two: FI choice percentages for each experimental phase (standard error).

Reward amount	Response effort	
	20 g	120 g
3 pellets	37 % FI Risk prone (2.0%)	30 % FI Risk prone (2.6%)
9 pellets	47% FI Risk prone (1.7%)	65% FI Risk averse (2.3 %)

A comparison of total average FI choices during phases one and five (low-effort/small-amount) revealed no significant differences ($t(11) = 0.71$, $p < .05$). As such, phases one and five were collapsed for the remaining analysis. A 2 (response effort) X 2 (reward amount) repeated measures ANOVA conducted on the percentage

of FI choice revealed a significant main effect of response effort ($F(1,11) = 9.18, p < .05$), a significant main effect of reward amount ($F(1,11) = 216.80, p < .05$), and a significant response-effort X reward-amount interaction ($F(1,11) = 40.28, p < .05$). Post hoc analysis (Tukey's HSD test) revealed that all pairwise comparisons differed significantly ($p's < .05$).

In order to verify the effects of increased effort requirements on choice, the average running distance during the low response-effort conditions was compared to the average of the high response-effort conditions. Subjects ran significantly less in the high-effort conditions compared to the low-effort conditions ($t(11)=8.61, p<.05$).

Discussion

Relative shifts in choice performance were created by manipulating the energy balance along two dimensions: response effort and reward amount. The data suggest that an increase in response effort requirements is effective at inducing shifts in choice preference. At low levels of effort, rats appear to behave in a risk-prone manner, regardless of reward amount. The low-effort condition failed to produce risk-sensitivity, and the overall pattern of response is reflective of a risk-prone tendency. The low-effort results are consistent with the majority of the literature in that when delay is manipulated, animals have a tendency to behave in a risk-prone manner (Bateson & Kacelnik, 1995, 1997; Caraco et al., 1992; Kacelnik & Bateson, 1996).

Increasing the response effort in the low-reward conditions shifted choice behavior toward the VI schedule. Interestingly, high-response effort also facilitated the occurrence of risk-aversion when reward amount was increased. The data suggest that the larger caloric costs associated with high-effort requirements force the subject to alter foraging strategy in order to meet environmental demands. Polar risk sensitivity is evident within the high-effort conditions. Past research may have failed to support the energy- budget hypothesis because manipulations of effort have been neglected.

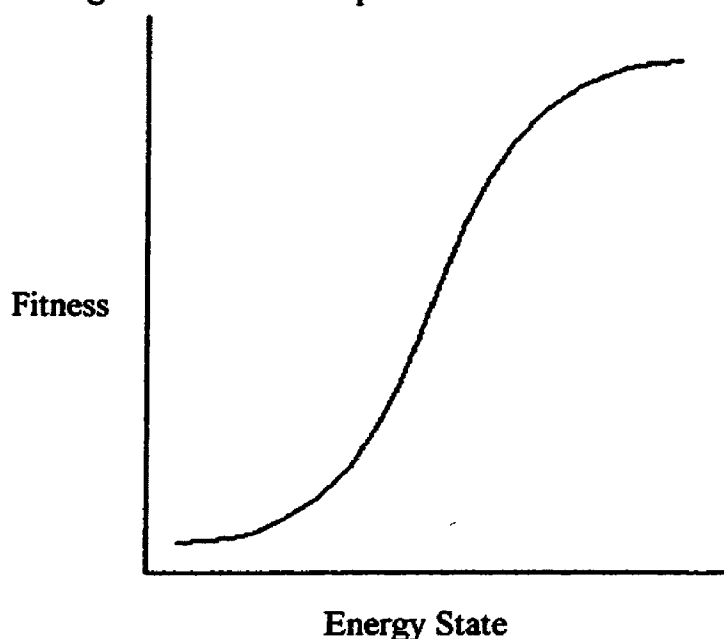
If increased effort requirements tax the energy state by depreciating immediate caloric intake, then it would be expected that the highest degree of risk aversion should

occur during low-effort/large-amount situations. However, it was discovered that within large-reward situations, the low-effort condition produced significantly *less* risk aversion than did the high-effort condition. Although this discovery may seem contradictory to the energy budget rule, these results are congruent with it. Relative shifts in performance are evident between the low-effort conditions with increasing risk proneness as reward amount drops. It seems that effort exacerbates the effects of reward-amount manipulations and the key to understanding how effort interacts with amount may lie in the relationship between overall fitness and the energy state.

One concept of the energy-budget rule depends on the existence of a sigmoidal relationship between fitness and energy balance (Caraco, 1980; Oster & Wilson, 1978; Real & Caraco, 1986; Smallwood, 1996; Stephens & Krebs, 1986). At two theoretical junctions, fitness asymptotes with the energy state, and gains within the energy balance become less likely to be reflected in fitness (refer to figure three). Within a certain range, small gains within the energy balance will have an enormous influence on fitness. It is likely that the energy budget rule (Caraco, 1980; Stephens, 1981) operates within the steepest domain of the sigmoidal curve. Animals that behave in a risk-sensitive manner may be functioning within the most extreme range of the sigmoidal curve, and may therefore be vulnerable to slight manipulations of the energy balance (Caraco, 1980). Situations that fail to simulate extreme environmental constraints, such as low response-effort conditions, may also fail to represent the influence of a changing energy budget on

fitness. In a low-energy expenditure situation, the response cost associated with foraging only minimally impacts fitness and the organism will survive regardless of minor changes in reward amount. Therefore, an organism foraging within a low response-effort environment is never forced to operate within the steepest domain of the sigmoidal function. High response effort exacerbates the effects of changing reward amounts by depleting caloric gains and increasing the probability of starvation. Thus, the energy budget model becomes more applicable when the costs associated with not altering foraging strategy are inflated.

Figure three: The sigmoidal relationship between fitness and the energy state.



Increased response effort may deplete energy reserves by minimizing immediate caloric gain. The data suggest that there is a caloric cost associated with increased response effort. The energy-budget model assumes that caloric costs have an effect on

fitness. A cognitive approach could explain the data in terms of the predicted likelihood of starvation. Organisms generate foraging decision rules based upon past experience and apply these rules to the current situation in order to maximize long-term gain. Increases in response effort may foster a prediction of rapidly approaching starvation. Thus, the organism is forced to alter foraging strategy abruptly in order to meet amplified environmental demands based upon the prediction that starvation is likely in the near future.

Changes in body mass should accompany the shift in foraging strategy from risk prone to risk averse. Throughout the experiment, post-session body mass was documented. Supplemental food was administered to maintain the subjects at 85% body mass during low-reward amount conditions (phases one, two, and five). During phases three and four, the subjects were receiving 100% of their daily intake within the experimental chamber due to the increased food rewards per trial. The average body mass of each subject was examined following the final session of phase four, and subjects had gained an average of 15g; a 5% increase from the phases that delivered a low amount of food per trial. Increase in body mass accompanied the shift toward risk-aversion between the high-effort phases, and decrease in body mass ushered in the shift toward risk-proneness/no preference between the low-effort phases. The animals were operating in a closed economy during the large-reward phases, and functioning in an open economy in all other phases (Hursh, 1980). The differences in experimental procedure do not present a

problem because research has shown that effects of economy are insignificant within a choice preparation (Logue, Chavarro, Rachlin, & Reader, 1988; LaFiette & Fantino, 1989).

Hamm and Shettelworth (1988) performed an experiment with pigeons in a free operant procedure with concurrent reinforcement schedules. The pigeons behaved in a consistent risk-averse manner even when the free operant procedure was altered to a discrete choice preparation. The authors conclude that risk aversion may be synonymous with behavioral impulsivity, given that the discrete-trials procedure is similar to those preparations used in experiments on self control. The data obtained from the current design are consistent with data obtained in a similar experiment using effort shifts and running wheels in a self-control procedure (Velkey, 1997). Impulsivity was discovered at low-effort levels and less impulsivity was obtained during high-effort levels. Given that increased effort requirements also increase risk-prone behavior, self control and risk proneness may be two overlapping behavioral phenomena.

A negative energy balance may force foragers to conserve energy by limiting the amount of effort exerted per response. When organisms behave in a risk-prone manner, they may be attempting to simultaneously limit the extent of the response required in order to obtain food *and* the time to the next rewarding event. Energy expenditure and caloric gain are inseparable factors therefore the organism may be treating the both the reward amount and the response as currencies. If responses are being treated as a currency, then it

is possible that the energy-budget rule may be operating within successive and simultaneous incentive contrast preparations. Slower running speeds conserve energy in low-reward amount conditions similar to how risk-prone behavior allows the organism to conserve energy in negative energy states. Positive contrast conditions may occur due to a greater accessibility of response-currency when the energy budget is positive.

Kacelnik and Bateson (1996) challenged researchers in the field of foraging theory by revealing the prevalence of the bidirectional nature of risk. The current design investigated their claim that delay variability, when isolated by invariant amount, produces constant risk proneness. Increased effort requirements revealed dramatic risk sensitivity, and future research should be aimed at analyzing the effects of increased effort conditions on manipulations of amount. Effort has been relatively neglected as a source of increasing energy expenditure within foraging experimentation. Risk-sensitive foraging may have been an elusive phenomenon in the past, but effort manipulation may be the key to unlocking the mysteries of foraging behavior. It is possible that a mechanism such as the energy-budget rule (Caraco, 1981, Stephens, 1981) is manifesting under higher effort conditions. Predictable patterns of choice become evident relative to shifts in reward amount during high-effort situations. It appears that increased reward amount successfully restores the energy budget crisis created by high-effort requirements. The economic relationship between caloric gain and energy expenditure may only be salient when higher costs are associated with foraging. However, the exact parameters of high

response-effort effects are unknown, and further research is necessary to determine whether less pronounced manipulations of effort will produce similar effects.

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Appendix

FULL LITERATURE REVIEW

The primary concern which living organisms face is sustenance. In order to survive, it is necessary for an animal to obtain resources. An organism's contribution to the next generation depends to some degree on its ability to forage in an optimal manner, and it is assumed that there is a heritable component of foraging behavior (Pyke, 1984). The relationship between foraging and fitness is dependent upon environmental constraints, and foraging strategy can be defined as choice between two or more patch alternatives. In the past, research has been aimed at dissecting the factors determining efficient foraging strategies, or what is called 'optimal foraging'. Optimal foraging theory assumes that fitness will be maximized by natural selection, and that fluctuations in the environment over a period of time may dictate a change in foraging strategy. The maximization of fitness will result in the maximization of foraging efficiency. Physical effort, time, distance, and overall caloric expenditure have been examined in this context (Appelzweig 1951; Collier, Hirsch, Levetsky, and Leshner; 1973; Keehn, 1981; Haddad et al., 1994). How much time and effort an animal expends on foraging is critical to survival, and it is conceivable that the animal may have a choice of what strategy to employ depending upon the existing environmental conditions. The fundamental question remaining is can a model sufficiently describe the influence of environmental factors on choice and thus predict foraging behavior?

It is crucial that an organism maximizes food intake and minimizes caloric expenditure, especially in an environment with limited resources. In some scenarios, it might be more adaptive for the animal to obtain food quickly and minimize the time delay between eating. In other situations, it seems that a less impulsive animal that decreases caloric expenditure by working a bit harder in order to obtain larger rewards might be more fit for that environment. Whether an animal chooses the smaller, more immediate reward or a larger, later reward may depend upon two factors: species-specific patterns of foraging, and environmental conditions. The decision an organism makes can be defined in terms of impulsivity or self-control; two opposite poles of the same spectrum.

Studies of impulsivity and self-control

Self-control may be an important factor guiding behavior in a wide variety of circumstances. Research on self-control in the past has traditionally involved a choice between a larger, more delayed reinforcement schedule, and a smaller more immediate reinforcement schedule (Skinner, 1953; Mischel, 1966; Rachlin and Green, 1972; Anslie, 1974). The preference for a lesser, more immediate reinforcement schedule has been called impulsivity. In contrast, the denial of the more immediate reward, and the preference for a delayed qualitatively or quantitatively better reinforcement schedule has been defined as self-control. Within the choice preparation, behavior has both costs and benefits, and the animal must compromise between minimizing the costs and maximizing

the benefits. According to optimal foraging theory (Pyke, 1984), an animal should preserve energy, or maximize caloric intake, given the existing environmental conditions. Pyke suggests that it would be more suitable for the organism to avoid risk and be more impulsive when resources are scarce. The omnipresent risk of starvation may impact an organism's foraging strategy in such a way that relinquishing an opportunity to eat may place the individual in jeopardy. If resources become more available, the environment allows the organism's foraging behavior to be more variable with a tendency to maximize caloric intake by displaying more self-controlled behavior.

Typically, pigeons show impulsivity in the traditional choice preparation (Rachlin and Green, 1972). In this particular investigation, the pigeons responded more frequently to the smaller, more immediate reward contingency than to the larger, more delayed reward contingency. Specifically, the subjects were given a choice between two keys that would allow access to food. Response to one of the two keys gave the subject within the experimental chamber immediate access to a time-limited amount of seed. Response to the second key allowed access to a larger amount of food but only following a delay. The subjects reliably preferred the more immediate condition, even though the delayed condition granted more food. Rachlin and Green were interested in whether an increase in delay shift foraging preference. In a second experiment, the researchers increased the fixed ratio and therefore increased the delay to reinforcement for both options. The change in procedure altered preference, and the subjects chose the larger, later

reinforcement contingency in more than sixty-percent of total trials. Examination of the data led Rachlin and Green to conclude that Herrnstein's (1970) matching law could account for this behavior. According to this model, the pigeon's behavior was guided by the availability of reinforcement, or in other words, the pigeons matched their performance with the relative change of reinforcement contingencies.

Ainsley (1974) found increased self-control in pigeons when they were given the opportunity to make an early, irreversible commitment to the larger, more delayed reward contingency. These experiments (Rachlin & Green, 1972; Ainsley, 1974) provided evidence that foraging strategy is not a fixed property of a given organism but that foraging preference can be altered by the specific experimental procedure.

Herrnstein's matching law describes a behavioral plasticity in which foraging preference will shift in accordance with a change in reinforcement contingencies (i.e. experimental procedure). The changes in behavior will only be as dramatic as the relative shift in procedure. Another model of choice behavior under consideration is the delay-reduction hypothesis proposed by Fantino (1969, 1982, 1987), which is essentially an extension of matching law to account for delays and exclusive preference. In accordance with optimal foraging theory, delay-reduction hypothesis predicts that an organism will adapt to changes in the delays associated with reinforcement, and the organism will exhibit exclusive preference under some delay combinations when it is beneficial to do so. One dilemma concerning the delay-reduction hypothesis is that the model is specific to

Fantino's (also see Lea, 1979) concurrent chain procedure, and it is difficult to say whether the model will generalize to other less restrictive preparations.

Ferster (1953) examined the delay of time between response and reinforcement in a VI schedule using pigeons. It was discovered that if the delay was short at first, and then gradually increased over many trials, there was no reduction in response rate. It may be inferred from these results that the effect of delay upon response is dependent upon the way in which the problem is presented to the subjects. Ferster's method of increasing or decreasing the time delay between response and reinforcement has become known as a 'fading' procedure. Mazur and Logue (1978) examined whether pigeons would exhibit exclusive preference for one of two alternatives. In an elegant experiment using a fading procedure, pigeons were able to make one of two responses enabling them to receive 6 sec access to grain or a 2 sec access to grain. Initially, the delay between the response and the 2 sec reinforcement amount was 6 sec, but was faded and eventually immediate access was granted. The data show that pigeons exhibit preference for the larger reinforcer (6 sec access) when the delays within the smaller reinforcement contingency are 3.25 sec or longer. Below the threshold of 3.25 sec, pigeons begin to select the more immediate food source, even though the reward is quantitatively less. It appears that choice is dependent upon the delay to gratification.

One of the many long standing debates regarding experimental procedure focuses on the validity of the behavior witnessed in the laboratory. Some biologists contend that

the behavior of food deprived subjects does not resemble the behavior of those same subjects in the wild. For the most part, subjects in psychological experiments are maintained at 80-85% of their free feeding body weights, and are allowed to forage for only a portion of their daily intake (Ferster, 1953; Fantino, 1969; Mazur and Logue, 1978 are some examples). These psychological experiments are said to resemble open economies in which food is readily available. Biologists tend to prefer allowing their subjects to forage 20h+ a day in situations which are accepted to resemble closed economies (Hursh, 1980), and are more representative of the natural environment. Logue, Chavarro, Rachlin, and Reader (1988) questioned whether a closed economy would affect an organism's choice behavior. The investigators placed pigeons in an operant chamber for 23h a day and allowed them to choose between the two traditional concurrent reinforcement schedules. The results showed that the pigeons behaved in an impulsive manner, and that economy may be insignificant in terms of its effect on behavior.

LaFiette and Fantino (1989) continued to examine whether the foraging economy in an experimental preparation would influence a pigeon's preference for two concurrent-chain reinforcement schedules. Performance was assessed under the two economic conditions described earlier. No systematic effect of economy was apparent on terminal-link responding. In both economies, terminal-link responding was significantly higher for the link which provided more frequent reinforcement. The data retrieved were consistent with the delay-reduction hypothesis; given either economic scenario, the pigeons behaved

impulsively.

In a continued effort to investigate the factors contributing to impulsivity, Grosch and Neurenger (1981) examined whether pigeons could be taught to choose the larger, more delayed reinforcer in six different experiments. Increased self-control was found in three conditions. First of all, the subjects behaved in a less impulsive manner when the reinforcer was not directly visible. Secondly, feeding the subjects just prior to testing increased preference for the larger, later alternative. Finally, preconditioning involving only the more delayed and more preferred reward influenced the subjects to behave in a more self-controlled manner during sessions where both options were made available.

Until recently, most self-control procedures have employed either pigeons or humans. Rats offer an opportunity to study a non-human animal that is more physiologically understood and similar to humans than their more popular counterparts. Rats are closer to humans phylogenetically, and they may help to provide some valuable insight into general mammalian processes. Tobin, Chelonis, and Logue (1993) conducted a series of experiments in order to assess self-control behavior in rats by implementing two different procedures. The first experiment used a discrete trial procedure containing an impulsive option (.1 sec reinforcer delay, 2 sec reinforcer access) and a self-controlled option (6 sec delay, and 6 sec access). The choice procedure was terminated only after each subject's preference stabilized for a period of five sessions. The rats behaved impulsively in the first manipulation, but the researchers wanted to know more about the

specific contributions of delay and reinforcer amount. In the second experiment, the delay to the larger reinforcer was adjusted incrementally during the session until the subjects exhibited no preference for either alternative. The generalized matching law was applied in this situation to determine the relative contributions of reinforcer amount and delay using the equation:

$$Sa/Sd = (\log D1 / \log D2) / (\log A1 / \log A2)$$

where Sa and Sd represent the organism's sensitivity to changes in procedure. The component Sa/Sd equals 1.0 when amount and delay exert equal control over behavior. Relatively smaller values of Sa/Sd pertain to lesser degrees of self-control. Matching law was used in this situation as a means of scaling the indices, but not a descriptor of choice. The results from this examination lead the researchers to conclude that the behavior witnessed was equally controlled by reinforcer amount and delay because the value of Sa/Sd obtained was .78 which is not significantly different from 1.0 [$t(14) = 0.85$, $p > .5$].

The relation between physical difference and impulsivity had not been investigated until an experiment conducted by Van Haaren , Van Hest, and Van De Poll (1988) tested sex differences using rats. Overall, the subjects preferred the larger, more delayed alternative. There was another interesting finding; male Wistar rats selected the larger-later reinforcement more frequently than their female counterparts. The

investigators suggest that females may be more sensitive to the delay to reinforcement than males, however, more research is necessary to determine whether this effect is attributable to sexual dimorphism or some other factor.

The impact of reinforcement type on behavior

Delay may not be the only factor influencing self-control. It seems intuitive that characteristics of the reward component of each contingency may influence behavior. Amount of reinforcement (frequency and volume) and an organism's preference for one type of reward over another, may be crucial factors guiding decision making processes. Rodriguez, Pena-Correal, & Mauro, (1984) and Mazur (1987) have shown that behavior in non-human subjects is sensitive to the amount of reward when delays are held constant. Non-human animals prefer immediate rewards even when the long-term rate of gain is reduced (impulsivity). The implication is that future rewards are devalued. Time discounting can be reversed if the delays to both the larger (more delayed) and the smaller (more immediate) rewards are increased (as demonstrated by Mazur and Logue, 1978). Benson and Stephens (1996) suggest that these findings are a function of how sensitive an organism is to timing. The discounting rate may be determined by 'the perceived likelihood that the forager will be interrupted from the foraging process' such that the larger, later reward is not guaranteed. It would be a greater risk to pass immediate food by in order to gain access to a larger supply of food later.

Most of the research on self-control in non-human subjects has revealed a

tendency toward impulsivity. In contrast, human subjects have typically exhibited self-control (Ainsley, 1974). Logue, Pena-Correal, Rodriguez, and Kabela (1986) gave humans of varying ages and gender a choice between the traditional concurrent reinforcement schedules. The researchers rewarded the subjects with points which could later be exchanged for money. The subjects reliably chose the more delayed, more preferred reward.

The study of self-control in humans has gained the interest of many clinical researchers because of its pertinence to social problems involving impulsivity such as gambling and addiction. In general, experimentation has revealed that humans seem to have a higher degree of self-control than non-humans. Many explanations have been offered for this difference in behavior. One explanation is that perhaps there is some qualitative, species-typical difference which allows humans to be more self-controlled. For example, humans have the ability to use rules in order to govern their behavior and make themselves less susceptible to environmental influences (e.g. Horne & Lowe, 1993; Sonuga-Barke, Lea & Webley, 1989). It has been suggested that humans use a counting strategy to determine which alternative will maximize (Kirk & Logue, 1996). Studies which support this hypothesis site an increase in self-control when children learn to read and write (Logue & Chavarro, 1992). Also consistent with the counting hypothesis was the finding that subjects became impulsive when auditory distracters (such as a radio playing in the background) were present during the experimental manipulation (Logue et

al., 1990). The contrast in behavior between humans and non-humans may also be attributable to species typical response systems; some species may inherently be more sensitive to the discounting effect that delay has on reinforcement value (Green, Fry & Myerson, 1994; Herrnstein, 1981; Rachlin, Raineri, & Cross, 1991; Rodriguez & Logue, 1988). Hyten, Madden, and Field (1994) suggested that the experimental procedure used in human studies may be viewed as a token reinforcement system. Decision making processes of human subjects may be dependent upon the delay to the exchange of reinforcement, but not upon the delay between response and reinforcement.

Jackson and Hackenberg (1996) questioned whether the contrasting results of self-control between humans and non-humans were due to the differential experimental methodologies employed. Research with human subjects has typically employed token reinforcement, while studies with non-humans have been conducted using only primary reinforcement. In order to assess this possible confound, Jackson and Hackenberg developed a methodology in which pigeons were exposed to a self-control procedure with token-like reinforcers. Choices resulted in the illumination of one or three LEDs. Each LED could later be exchanged for 2 sec access to food. The one LED stimulus was delivered immediately and the three LED array was delivered after a 6 sec delay. Jackson and Hackenberg found that delay to reward had less of an influence on behavior than the delay to token presentation. Therefore, token reinforcement seems to promote self-control in humans and non-humans. The differences in self-control shown in the past

between humans and non-humans may be partially due to the procedural differences employed in assessing these characteristics.

Once again, we are lead to the unrelenting question of how experimental methodology influences choice behavior. Siegel and Rachlin (1995) analyzed the differential effects of FR and FI on self-control using a 'soft-commitment' procedure. Two keys provided pigeons access to either an impulsive (0.5 s delay for 2.5 s food access) or a self-control (3.5 s delay, 4.5 s access) option, the ITIs were 5 s given either response. During the baseline concurrent CRF condition, each pigeon was allowed to choose between either option by pecking once at either key. The procedure was changed in following phases by implementing a FR 31 schedule, and then a FI 30 schedule. There were two criteria for changing the procedure to a different schedule: fifteen trials must have elapsed, and the same alternative must have been chosen at least fifty-percent of the time over the final five trials. A significant main effect of schedule was revealed by a repeated measures analysis of variance, $F(3,9) = 12.93$, $p < .01$. re immediate reward. The highest amount of self-control was apparent during the CRF condition. Both the FR and FI conditions produced self-control, however there was little difference between the two. The indifference between the two schedules may be due to evidence that initial preference at the beginning of each session remained constant throughout the remainder of the trials under that condition. The researchers suggest that the subjects commit to a response procedure because alternating between strategies may result in energy loss.

Choice does not seem to be differentially influenced when both options are either simultaneously fixed intervals or fixed ratios. Chelonis, King, Logue, and Tobin (1994) investigated two models of delay discounting using pigeons and a multitude of VI and FI combinations. One discounting model proposed by Mazur (1984) predicts that the value of a given outcome is negatively related to delay, but positively related to reinforcement amount. Three predictions are derived from Mazur's model. First, the subject will show a preference for variable delays over fixed delays, and second, that the function of delay upon preference will be hyperbolic in nature. Third, reinforcement and delay will have absolute influences upon behavior. The other model examined in this study, Baum's (1974, as cited in Chelonis et al., 1994) modified version of the generalized matching law, describes that the function of delay upon preference will be negatively accelerating and relative to the subject's experience. The first phase of the experiment examined choice by maintaining the reinforcer amount at 4.5 s under both options, while the delay for one options remained fixed while the other varied. Pigeons preferred the more variable delay in this circumstance. In subsequent conditions, the impulsive and self-control options were modulated on nonindependent concurrent FI and VI schedules respectively, separated by a 3 s changeover delay. The delay to reinforcement for both options was manipulated in fourteen different experimental conditions, and it was discovered that the degree of self-control behavior increased as the delay increased. The function of delay upon preference was discovered to be negatively accelerating. These results provide support for the

generalized matching law modified by Baum (1974). The researchers suggest that hyperbolic discounting models are best applied in situations where both the amount and delay are increased. Ultimately, both models predict a preference for the variable, self-control option, however the data from this experiment conform better to the generalized matching law.

Species specific response patterns may be revealed as the exploration into self-control continues. The physiology of an organism may predispose it to behave in an absolute fashion when challenged with situations that engage an appetitive system. Researchers have questioned the factors which contribute to the stability of self-controlled behavior, and they have also investigated the processes underlying these preferences using inferential and mathematical models. So far, reinforcement delay and amount have been examined within the context of self-control, however it appears that other factors may influence foraging behavior as well.

The Effects of Effort

Many of the experiments discussed so far have focused on the delay of time between response and reward. Intuitively, time may play a critical role in foraging behavior because shorter delays between rewards translate into greater opportunities for maximizing caloric intake. Increasing delays may have something in common with the effort required to gain access to resources. Effort is traditionally conceived as a physical

force requirement, but in general, when effort is increased the organism's energy reserve is decreased. Physical force may not be the only component affecting an organism's perception of effort. For instance, people are always interested in saving time while running errands, and they will choose a driving route which is perceived as being the shortest distance because that saves time. The physical force required to drive a car is minimal and therefore may have no effect on the decision process. The time lost during driving is effortful because it is taxing on energy stores. The example can be related to non-humans foraging in the natural environment where a large amount of distance may separate two food patches. Though it takes physical force to transport from one food source to the next, the amount of time spent doing so may be the critical factor rather than the minimal physical requirement itself.

In the laboratory, effort can be defined as the number of responses required in order to obtain a reward. Applezweig (1951) presented rats with several levers, each demanding a different degree of tangential force. The results show that higher degrees of tangential force slow learning, and the learned response in the higher effort levels is more vulnerable to rapid extinction.

Lewis (1964) found that rats pulling a weighted harness down a runway would run faster and consume more food in the goal box than less restrained rats. The high effort experimental group pulled a weight of 80g and the low effort group pulled a weight of 5g. Lewis proposed several interpretations of these results. First, the subject may

attribute a higher value to the reinforcer due to the high degree of effort required to obtain it. Secondly, the high effort requirement may cause frustration and increase the drive level of the subject, thus increasing the reinforcement value (the reinforcement value must equal the drive level in order to reduce the drive). Finally, the effort expended heightens perception and acts to raise the value of the reinforcement. In any interpretation, Lewis suggested that the increasing value of the reward facilitates the subject's goal-directed behavior.

In contrast to Lewis' findings, Collier, et al. (1973) found that higher effort requirements negatively impact rates of response. The researchers studied the running rates of rats in two procedures: in a running wheel and on a motorized belt at various inclinations. The rats ran for shorter distances given a higher effort requirement in either apparatus. Collier et al. suggest that effort decreases response rate. Keehn (1981) confirmed that effort decreases response rate when rats are given an option between two levers. When the effort requirement for one lever increases, the response rate to that lever decreases and the response rate to the other lever increases. Furthermore, Alling and Poling (1995) conducted a study which examined the consequences of differing FR schedules under various effort requirements. Higher effort requirements were found to impact response rate regardless of the FR.

Brooks (1994) conducted an experiment using the running wheel in order to investigate the effects of effort. Rats were required to run varying distances in two

different tangential force conditions (20g or 80g of tangential force was necessary to move the wheel). Each subject was exposed to all combination of distance and tangential force. It seems that the response is determined by the tangential force requirement and is relatively unaffected by distance. Greater distance was associated with longer post-reinforcement pauses, and it is suggested that distance is related to response cost; having little effect on on-task performance. This study also suggests that tangential force, or response force, acts directly upon response rate. Brooks suggests that effort can be defined in two ways: response cost or response force.

Response cost and ratio duration may serve the general role as a time cost. Increased response cost and increased ratio length in a choice preparation both permit the subjects to be more impulsive. As either variable decreases, responding becomes more self-controlled. If all else is held constant, and the size of reinforcement is decreased, impulsivity is also found. In general, when response force is increased, the rate of response decreases as a result. Impulsivity is also found when a primary reinforcement procedure is used, however, Jackson and Hackenberg (1996) found that when a token-like economy is used with pigeons, the subjects display more self-control. It has not yet been determined how a token economy procedure would affect the performance of other species. In addition to this, more investigation is necessary to determine how distance requirements influence response. Brooks suggested that distance in the running wheel is associated with response cost while Collier et al. have suggested that distance may be an

aversive effort condition which decreases overall response.

Certain behavioral tendencies develop when an organism is presented with two options and faced with decisions concerning caloric intake. Organisms exhibit a spectrum of behavioral tendencies dependent upon the particular experimental methodology used. The self-control literature describes behavior when two options differ in the speed and the amount of reinforcement. These dimensions are only minimally representative of the limitless foraging possibilities that can occur in a natural setting. In an attempt to understand the constellation of foraging strategies employed by animals, a review of the behavioral ecology literature is warranted to get a contrasting perspective on foraging behavior.

Risk-prone vs. risk-averse behavior

Psychology and ethology were originally interwoven fields, but the development of each discipline created a chasm between them. The two have reunited only recently in an effort to understand behavior in the context of ecological pressure. Behavior is a reflection of an evolutionary history, whether it occurs within a laboratory or within a natural setting. Many researchers (Timberlake, 1994; Shettleworth, 1994; Kamil and Roitblat, 1985) believe that the two disciplines must merge in order to fully understand the functional and mechanistic aspects of behavior.

Foraging strategies are dependent upon characteristics of the environment and the

species. The strategies that an animal utilizes are in part determined by the availability of, and the variability within, resources. It is assumed that natural selection favors individuals that forage efficiently. Caraco's (1980) utility theory predicts that choices between a more variable patch (risk-prone) and a more consistent patch (risk-averse) should be dependent upon resource availability. The utility model can be best summarized not in terms of the maximization of intake, but in terms of the minimization of the risk of starvation. A preference for a more variable patch promotes vulnerability and leaves the animal more prone to the risk of starvation.

Utility theory predicts that an organism's choice will be dependent upon mean food availability. Stephens (1981) proposed an analytical model which is similar to utility theory, but includes an additional component which accounts for systematic foraging. The predictions produced by the analytical model adjust as the organism obtains resources. The analytical model predicts that risk-prone behavior is suggested to be less likely when few decisions remain. For instance, consider an experimental procedure with a fixed amount of foraging time. According to this model, risk-prone behavior should decrease as each session progresses. Stephens suggests that the animal has a concept of a time horizon, and the approaching time horizon serves as a cue to decrease a preference for a more variable patch.

McNamara (1982) suggests that foraging is dynamic, and an animal must switch back and forth between risk-prone and risk-averse behavior in order to forage optimally.

McNamara's theory of stochastic foraging describes that current energy reserves may dictate the type of strategy employed. Foraging is limited by how accessible resources are and how much time the animal has to forage for those resources. In the experimental setting, the duration of each session limits which strategies can be employed. If a session is short, and the number of rewarding events to occur is small, preference is dictated by immediate net energy gains. Animals that have rapid metabolisms are extremely sensitive to experimental manipulations. For instance, hummingbirds or shrews need to spend the majority of the time foraging in order to consume an ample supply of food for the night. In such scenarios, it is crucial to save time between food patches. McNamara and Houston (1982) suggest that an animal with a high metabolism will behave in an impulsive manner by choosing less variable patches, therefore minimizing the risk of starvation overnight. Animals with slower metabolisms may be risk-averse at the beginning of each session. However, as the animal's energy reserve is saturated, a preference for the more variable patch may develop. Another variable contributing to risk-averse behavior is the time cost associated with a shift in preference. The energy expended during a switch-over delay is a considerable influence guiding an organism's foraging behavior, and perhaps this is why concurrent chaining procedures promote exclusive preference.

When animals are faced with two options that yield the same rate of energy gain, yet differ in payoff variances, it has been demonstrated that animals prefer one food source over another. Preference for one option can then be analyzed in the dimension of

variability. Caraco (1981) analyzed how an animal's energy reserve may influence risk-prone behavior. In two experiments with yellow-eyed juncos (*Junco heymalis*), the birds were exposed to a series of trials containing constant vs. variable rewards. For example, during the course of one session, the birds could choose between a constant (2 seeds per trial) reward at one feeder, or a more variable (0-4 seeds per trial) reward in a second feeder. The subjects showed consistent preferences for the constant feeder when food intake was in excess of energy expenditure. A circumstance of an excess supply is described as a positive energy balance. If the organism's current energy reserve influences preference, then food deprivation should result in a change in foraging behavior. The juncos behaved in a risk-prone manner when the average rate of energy expended was greater than the average rate of food intake. The results lead Caraco to propose that risk-prone and risk-averse behaviors are directly related to the current energy budget. It seems counterintuitive that an organisms would deliberately increase its own vulnerability to starvation when energy stores are low by behaving in a risk-prone manner. However, the more variable alternative will yield a larger supply of food occasionally, and a run of good luck could solve the crisis of a negative energy balance.

The results revealed by Caraco instigated a profound interest in behavioral sensitivity as a function of energy reserves. Barnard and Brown (1984) tested behavioral sensitivity in common shrews (*Sorex araneus*) using concurrent feeding sites; one fixed amount and one variable amount. The shrews were enclosed in plastic tanks with two

feeding stations. Each session was composed of twenty trials, and the shrews were given supplemental food between each session. The transition from risk-averse preference (60%) to risk-prone preference (74%) occurred when the shrews were fed an amount which was below their physiological requirement. Whereas most other experiments have examined foraging behavior using small birds in a laboratory setting, this experiment demonstrated that a small mammal is sensitive to risk within an open economy.

Caraco (1980) proposes a variance discounting model in which a forager should maximize caloric intake according to the uncertainty of the reward. This model argues that the forager should be willing to ignore the constant reward only when a high mean accompanies the variable option. When the mean amount of the reward is low, the forager should prefer a constant reward. According to this model, foragers should maximize:

$$F = \mu - k\sigma$$

where μ is the mean food reward, k is the constant of risk-aversion, and σ is the variance in food reward. The constant of risk-aversion is understood as the degree to which the variable option is evolutionarily or behaviorally undesirable. As μ increases it compensates for k , and risk-prone behavior results.

Originally, risk sensitivity caused foraging theorists to reconsider the assumption that mean reward amount could consistently and accurately predict behavior. It is unclear how an organism would respond when both the mean amount and the amount of variance are manipulated. The variance discounting model predicts constant risk-aversion when

both options supply equivalent amounts of food regardless of the degree of variance.

Stephens and Charnov (1982) propose the z-score model to account for a variable reward preference when both options vary in food amount and degree of variance, and total food gains can be represented as a normal distribution. The z-score model describes that the forager minimizes the probability of resource insufficiency by minimizing:

$$z = \frac{R - \mu}{\sigma}$$

where σ is the standard deviation of food reward and R is the amount of food that the forager requires.

Stephens and Paton (1986) examined the applicability of the z-score model by placing six wild-caught Rufus hummingbirds (*Selasphorus rufus*) in a free choice preparation with two options. One option yielded a high mean amount with a high variance while the other yielded a low mean amount with a low variance. Microcentrifuge tubes located behind flowers administered sugar water to the subjects, and photocensors signaled when a subject had visited a particular site. Once preference was established in the low-line condition, the means of each option increased by the same amount. Risk-prone tendencies were observed in the low-line treatment, and preferences shifted to the more constant alternative (the low-variance condition) when reward amount was increased. Constant risk-aversion was not demonstrated, therefore the variance

discounting theorem cannot be applicable. The z-score model predicts that a preference for the more variable alternative should be stronger in the low-line treatment than the high-line treatment. The findings are consistent with others (Barnard & Brown, 1985; Caraco, 1980) which demonstrate that risk-proneness occurs when energy expenditure exceeds expected caloric gain. The z-score model appears to account for the shift toward risk-prone foraging behavior when both the mean amount and the amount of variability are manipulated.

A food patch can vary in a variety of dimensions. Researchers had manipulated the amount of food and the delay to reward, yet none had varied the quality of food. Tuttle, Wulfson, and Caraco (1990) found significant risk-sensitivity with white-throated sparrows (*Zonotrichia albicollis*) when the birds were exposed to a situation involving constant and variable rewards having equivalent means, but unequal qualities.

Each subject was housed separately in aviaries. Each aviary contained two chambers; a test area and a living area. Within the test chamber, the subjects were presented with 24 small dishes all containing grit and some containing small seed. Each dish was covered with a weighted, colored lid that the sparrows were expected to remove in order to gain access to the food. One lid color was associated with the consistent reward, while the other was associated with the variable reward during pretesting. The sparrows were deprived of food for the first two hours of a ten hour foraging day. During a test session, a trial ended when the subject had made 12 choices, or five minutes had

elapsed. A 15 minute deprivation period separated each of the six trials constituting an experimental session. Each subject spent no more than 1.75 h per day in the testing chamber. Initially, the sparrows exhibited risk-prone behavior, but as the subjects progressed through the sessions and regained an energy reserve, risk-averse behavior became dominant. The researchers allowed the subjects to forage in excess of their daily requirement, and by the third day of testing, almost exclusive preference for the more constant reward developed.

Several field studies have been conducted which have outlined other factors influencing risk sensitivity. Caraco, Uetz, Gillespie, and Giraldeau (1995) found that an individual's resource consumption is dependent upon the size of its social group. The researchers discovered that an individual spider's food consumption is inversely proportional to colony size, thus risk sensitivity is modulated by the formation of a social group. Similar functions are apparent among social groups that form inconsistent social bonds. Some ethologists suggest that migratory birds form a more cohesive social network while migrating than when not migrating. Bednekoff and Houston (1994) noted that risk-proneness in birds (*Dendroica coronata*) facilitates premigratory fattening. Alternatively, the birds exhibit risk-averse tendencies during the rest of the year when they are not migrating.

Field study offers the opportunity to witness the constellation of factors which contribute to foraging behavior. According to Stephens (1981), the minimization of the

probability of starvation explains both risk-averse and risk-prone foraging behavior. However, the avoidance of starvation may not be the only factor driving foraging strategy. McNamara, Merad, and Houston (1991) have suggested that the relationship between fitness and energy reserve is non-linear, thus no single model can predict foraging preference. Gender differences support this rationale. Organisms are not only concerned with sustenance, but also fitness, and therefore reproduction must also be a factor when considering the depletion of energy reserves. Sensitivity to risk increases as a function of the abating energy reserve, or cost, associated with reproduction. Another factor underlying risk-sensitivity may be the relationship between energy reserves and reproductive success.

One failure of the laboratory setting is the inability to simulate an environment which is indirectly related to the foraging problem. Food deprivation is only one method of depleting an organism's energy balance. In the natural environment, weather changes profoundly impact resource availability, and may influence foraging strategies as a result. McNamara (1996) argues that risk-averse behavior is the best method of maximizing survival during an arduous season such as winter. As a consequence of climatic change, less risk-prone behavior should occur than predicted by models in which the environment is not considered. McNamara stresses that animals approach foraging problems with a single, complex decision rule based on past experiences and current physiological states. An animal in the natural environment is likely to respond to a string of bad luck as an

indication of depleted resources. The organism struggling to survive in a harsh environment should become averse to risk. Furthermore, there exists a need for an organism to learn about its changing environment. The necessity to learn is likely to reduce risk-prone preferences because more variable food options offer less information per unit time than do constant alternatives.

Most foraging animals, especially those commonly used in the laboratory setting, are time sensitive. Therefore an organism is likely to choose the more variable option (risk-proneness) because it will yield a smaller delay half of the time. Ha (1991) performed an experiment using an operant chamber and gray jays (*Perisoreus canadensis*). Concurrent VR schedules differed between experimental groups (VR10, 20, 40, and 80), and both options supplied equivalent amounts of food. The jays were expected to hop between two perches in order to receive reinforcement. Metabolic rates were forcefully increased by placing the subjects in a -23 degree Celsius chamber during each night of testing (perhaps the researcher was afraid that the jays would putrefy if not refrigerated). It was expected that lower temperatures would promote risk-prone tendencies by increasing the subject's metabolic rate and deplete their energy balance. The results demonstrate exclusive risk-prone behavior across the various VR conditions. These results are contradictory to data obtained in other experiments involving small aviary species in which risk-sensitivity was discovered. The researcher implies that the sensitivity found in other species is created by the compound effect of varying both delay

and amount simultaneously. Caraco et al. (1990) addressed this issue as a possible confound, and manipulated the ambient temperature and the mean amount of seed supplied to yellow-eyed juncos. The juncos preferred the more constant option when their energy budgets were negative, and showed only a slight preference toward the variable option when their energy budgets were positive.

Both greater expected reward and reduced expected delay influence foraging preference, but it is unclear how the relationship between reward amount and delay affects foraging behavior. Caraco, Kacelnik, Mesnik, & Smulewitz (1992) proposed a model which predicts risk-proneness when the delay is varied, and risk-aversion when the amount of reward is varied. Furthermore, when both delay and amount are varied, a positive delay-amount covariance will produce risk-aversion, and a negative covariance will produce risk-proneness. Bateson and Kacelnik (1996) have found evidence throughout the literature of bi-directional foraging based upon the factor which is varied. Risk sensitivity occurs in extreme instances in which a rapid metabolism is manipulated by dramatic measures. Risk sensitivity is clearly found in short-term maximizers, but evidence that foraging preference is malleable is not as compelling in larger animals.

The majority of experiments investigating risk-proneness have employed only small birds, and it remains to be seen how other animals will respond in such a scenario. Mazur (1988) suggested that a tendency toward risk-proneness would occur if an organism was relatively insensitive to reinforcement probability. In this experiment, rats were given a

choice between two levers: a constant alternative and an adjusting or variable alternative. Rats showed preference for the more variable alternative (risk-prone), but when reinforcement amounts were increased, the rats shifted their preference toward the more constant reward (risk-aversion). Therefore, risk-proneness decreased with increasing reinforcement amounts. Mazur denies that these results show a systematic relationship between energy balance and risk-prone behavior, and claims that risk-proneness is altered only by quantity of reinforcement.

Specific cognitive processes allow animals to form representations of their environment. The organism will depend on representations in order to compute decision rules. It is assumed that decision rules serve an adaptive and evolutionary function by increasing the probability of survival. Kacelnik and Bateson (1996) suggest that a cognitive approach and a behavioral ecological approach be fused in order to understand the decision rules animals generate while foraging. First of all, they state that when risk is a result of variability in the amount of reward, animals most frequently display risk-averse preferences. If the variability lies in the delay to reward, animals are universally risk-prone. Risk sensitive foraging theory is acknowledged by the authors as the most accurate and current method of understanding how an energy budget will affect performance. In addition to this, the authors have combined an information-processing approach with Weber's law in order to account for risk-sensitivity. Weber's law is the principle that the accuracy of perception decreases proportionally to stimulus value and intensity, thus there

is an optimal level of perceptual accuracy. Stimulus value is plotted against the accuracy of perception to provide a normal distribution. Weber's law provides the foundation for a theoretical framework that accounts for time variables, known as scalar expectancy theory (SET; Gibbon, 1977 as cited in Kacelnik & Bateson, 1995). Reborda and Kacelnik (1991) have expanded SET to include representations for amount as well as for delay variability. The value remembered for an interval or amount is represented as a normal distribution. Each subsequent trial is compared to the distribution and a choice is made according to an expected gain or loss. SET predicts for exclusive preference by an organism dependent upon whether delay or mean amount is varied. Specifically, SET predicts that variability in delay should be preferred because the variable option will often yield shorter delays without compromising long-term gains by supplying more food within a shorter period of time. Variability in amount, on the other hand, should be avoided because the probability of the constant option reoccurring is much higher than the probability of the variable amount reoccurring. Bateson and Kacelnik are zoologists, yet they have adopted a psychological model to account for risk sensitivity. Here is a clear example that the distinctions separating ecological and psychological disciplines are eroding. The authors recommend that 'only a fusion of functional and mechanistic thinking will lead to progress in the understanding of animal decision making.'

In order to examine SET, Bateson and Kacelnik (1995) tested starlings (*Sturnus vulgaris*) under two different preparations in which the fixed option remained constant

(5 unit reward after 20 seconds). In treatment A, the inconsistent option varied in reward amount (3 or 7 units with equal probabilities after 20 s). In treatment D, the delay of time to reinforcement was varied (5 units after either 2.5 or 60.5s). The results showed that the subjects preferred variable delays when reinforcement amounts were equivalent, and variance in amount was avoided when the delays were the same. The data support SET in that the starlings displayed almost exclusive preference within each preparation.

In a further analysis of the effect created by variance in delay, Bateson and Kacelnik (1997) investigated how commitment and the ability to predict caloric gain would influence risk sensitivity. Rather than a choice resulting in a single amount of food, each choice lead to a chain of six delayed food items. Choosing the fixed option resulted in a chain of equal delays, and choosing the variable option resulted in a chain of either long or short delays. The starlings were divided into two groups: a risk free group in which the choice for the variable option yielded predictable delays, and a risky group in which the choice for the variable option resulted in an unpredictable chain of random delays. Both groups exhibited risk-prone behavior throughout the experiment. During a second phase of the experiment, the rewards obtained from each group were increased in order to force the subjects into a positive energy balance. Counter to the predictions of the energy budget rule, no effect of budget on performance was found in either group.

Many researchers have pointed out that the only way to establish preference independent of reward amount is to make both the constant and the risky option yield

equivalent amounts of food. If both the variable and the fixed outcome have the same mean it is also easier to control a subject's energy balance. Hamm and Shettleworth (1987) examined how pigeons react given one fixed alternative and one variable alternative in a free operant procedure. Both options administered reinforcement on concurrent VI 60 schedules. The variable alternative differed in reinforcement amount (0-4 food pellets) while the constant alternative continually granted 2 food pellets. The results reveal that the pigeons were risk-averse under conditions which generated variance by manipulating reinforcement amount. In a second experiment, the procedure was altered from a free operant to a discrete trial preparation, all other conditions remained the same as in the first experiment. The risk-averse tendencies in the first experiment were magnified within the discrete trial procedure. The researchers concluded that the discrete trial procedure was similar to preparations employed to evaluate self-control because the variable reinforcement delivery may yield more food per unit time than the constant alternative. As each session progressed, risk-aversion became more prominent. The experiment conducted by Hamm and Shettleworth revealed data similar to other experiments that generated variability by controlling reinforcement amount.

A review of the behavioral ecology literature has revealed no standardized procedure for examining risk sensitivity. Procedurally, the only requirement found throughout the literature is the necessity for one option to be more variable than the other option. An analysis of the self-control literature suggests that economy is relatively

insignificant. Case, Nichols and Fantino (1995) investigated whether risk sensitivity was independent of economy. The researchers found exclusive preference for the more variable alternative in an experiment using concurrent-chain FI/VI terminal link water schedules under differing economies. The researchers conclude that risk preference is unaffected by the economy, and these results are consistent with other findings regarding closed economies and foraging behavior (LaFiette & Fantino, 1989).

The literature surrounding risk sensitivity has demonstrated that the degree to which an animal behaves in a risk averse or prone manner is dependent upon whether time or amount is experimentally manipulated. When variability is generated by the delay of reward animals are risk-prone, and the degree of risk-proneness is relatively unaltered by an increase in energy budget. Alternatively, when variability is generated by the amount of reward, animals are usually risk-averse and there is some evidence that the organism's energy budget effects preference. There exist many gaps in the literature, and it is necessary to compare the effects of delay and amount in the same species under consistent experimental preparation. The precise dynamics of risk sensitive preferences have not been established, and to date, none of the current theoretical frameworks allows generalization across different situations. The factor which has fueled much of the recent interest in risk sensitivity are the effects witnessed after altering an organism's energy balance. A closer examination of the underlying ecological, physiological, and psychological processes contributing to foraging may prove to be profitable adventures in

a joint quest to understand behavior.

Overall, very few studies have demonstrated risk-sensitivity. Studies conducted with relatively larger animals with slower metabolic rates have failed to show sensitivity to energy budgets. Larger animals have a larger energy reserve and may not be susceptible to minor changes in experimental procedure aimed at shifting preference. Naturalistic observations have shown that factors other than amount and time variability impact foraging preference. There has been no research directly aimed at examining the effects of effort on risk sensitivity, and effort may be the defining variable determining an organism's energy balance.

Theoretically, self-control and risk-proneness may lie on two overlapping continuums of behavior in which impulsivity may equate risk-aversion. Energy expenditure may influence choice given one constant and one variable alternative. Specifically, it is not understood how increased effort levels will affect foraging strategy when amount of reward is held constant and delay is manipulated. An experimental procedure with rats and a choice between two running wheels, one variable interval and one fixed interval schedule of reinforcement, may help further refine the converging theoretical models of foraging behavior. In a low effort condition, selection between the two wheels should be risk-averse (preference for the constant reinforcement schedule). The amount of effort required to obtain food may impact an organism's energy balance, and thus may influence foraging strategy. Increasing the amount of energy required to

obtain food may promote risk-prone behavior by depleting the energy balance. Thus, increasing the effort requirement in both running wheels may shift choice to the more risky, or variable, alternative. Increasing the quantity of reinforcement in both conditions may counteract the effects of an increased effort requirement and restore a positive energy balance, thus promoting risk-averse behavior.

Rats have a tendency to be impulsive and averse to risk in the context of starvation. In general, animals often exhibit a preference for a variable option (risk-prone behavior) when delay is manipulated. Therefore, combining a variable delay preparation with an animal that tends to behave in a risk-averse manner should produce a volatile state in which the organism is sensitive to risk. It is hypothesized that the subjects will predominantly favor the constant reward option (risk-averse) during the low effort condition and will shift toward the variable alternative when the effort requirement is increased. It has been demonstrated that performance within a choice paradigm is altered when effort requirements are shifted from 20 to 80g tangential force (Velkey, 1997). The rate of acquisition and asymptotic running speeds diminish with high effort levels (Haddad et al., 1993). In order to deplete the energy balance substantially and shift preference, effort should be increased above 80g, yet less than 160g. Therefore, dividing the difference in half (to 120g) should adequately shift preference. The third and final phase is designed to examine whether increasing reinforcement will reinstate a positive energy balance under a high effort requirement. Allowing the rats to forage for 100% of their

intake would make it difficult to manipulate energy reserves by increasing the effort requirements; therefore the rats will be maintained at 85% of their free feeding body mass under all experimental conditions. After schedule requirements are met, a brake will restrain the opposite wheel making it impossible for the subjects to alternate between options. A brief intertrial interval will be used to establish a uniform break between trials due to the discrepancy in handling time between experimental phases.

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